



Intra-country introductions unraveling global hotspots of alien fish species

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Abstract

Alien or non-native species are defined as species living outside their natural distributional ranges. The spread of alien species is increasing globally as a result of rapid technological advances and globalization. Recent investigations have estimated global hotspots of alien established species on the basis of geopolitical boundaries, including Dawson et al. (in: *Nat Ecol Evol* 1:186. <https://doi.org/10.1038/s41559-017-0186>, 2017). In particular, these investigations do not consider Intra-Country Established Alien Species, i.e., successful introductions that occur among regions within the same country. In continental countries such as Brazil, the USA and China, studies excluding Intra-Country Established Alien Species (IEAS) waste essential information. Here, we argue that researchers should also consider intra-country introductions when estimating and addressing the risks of alien introductions. By using detailed data for freshwater fish including IEAS in large countries, we demonstrate that novel hotspots for IEAS have arisen worldwide. We illustrate emblematic examples of IEAS, as well as their vectors and negative impacts, to demonstrate the range of impacts that might be missed when excluding IEAS data from analysis. We recognize the need for generalizations, but generalizations based on incomplete data can misinform conservation efforts, particularly in megadiverse regions. Ignores IEAS influences how we count non-native species, invasions and perceive invisibility and impacts. Consequently, upcoming records and analysis of invasion patterns and management of aliens and IEAS global hotspots must account for such biases in quantifying the IEAS portion.

Keywords Conservation policy · Watershed · Global assessment · Invasion risk · Spatial grain · Geographic distribution · Non-native species

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Introduction

A species is considered native to a given region if its presence is the product of natural processes (e.g., without human assistance), and colonization or invasion of new geographic regions has occurred naturally, either by passive or active transport. However, many species are increasingly being observed outside of their natural range as a result of human-mediated introductions; these have been designated as non-native or alien species. In other words, alien or non-native species are defined as species living outside their natural distributional ranges, even if introduced from other conterminous within a single country (Guo and Ricklefs 2010). Once an alien species establishes a new self-sustaining population outside of its natural geographical range, it becomes an Established Alien Species (EAS). The number of EAS has substantially increased around the world over the last 50 years, as a result of globalization and economic development (Seebens et al. 2017), and has contributed to nearly 40% of global animal extinctions (CBD 2017). More recently, the impacts of EAS have been the subject of intense scientific research, but our understanding of the invasion process is still developing, especially with regards to megadiverse regions, and this knowledge gap has resulted in the application of inappropriate conservation measures (Parker et al. 1999; Frehse et al. 2016).

Macroecological studies have substantially advanced our understanding of factors that might contribute to the geographic range and likelihood of establishment of invasive species. However, the analysis of such large datasets requires consideration of the spatial scale, since the results and interpretation can differ depending on the granularity of the data used (e.g., Simberloff 2004; Fitzgerald et al. 2016; Tarasi and Peet 2017). Clearly, geopolitical divisions are generally artificial and not relevant for ecological understanding, although some country borders do follow natural geographic divides such as rivers or geological formations, and yet researchers commonly use country boundaries to classify species as native or non-native (Rahel 2000; Bezerra et al. 2019), regardless of whether the boundary actually represents a biological barrier to invasion and establishment. While geopolitical borders may be important for policy decisions and management, their use in analyzing patterns of species distribution requires further scrutiny. In particular, defining whether a species is an alien species based on its distribution at the national scale may be too coarse a scale to accurately model species invasions. In a recent study, Dawson et al. (2017) compiled an extensive dataset of EAS, and provided a valuable and comprehensive inference of global hotspots of EAS. However, the analysis was based on geopolitical divisions, which may impact conclusions on species invasions. To further investigate this issue, we here re-analyze the data for freshwater fishes from Dawson et al. (2017) and show that redefining the EAS inclusion criteria in the analysis results in substantially different conclusions.

Dawson et al. (2017) did not consider Intra-Country Established Alien Species—IEAS, i.e., successful introductions and establishment that occur among regions or in a novel region within the same country. In continental countries such as Brazil, the USA and China, studies excluding IEAS frequently waste significant information, since such IEAS may be effective invaders, and the absence of data on IEAS may substantially reduce our power to detect factors influencing invasion potential (e.g. Bezerra et al. 2019). Information concerning EAS and IEAS is available, at least for freshwater fish, in the data sources used by Dawson et al. (2017) (I3 N database, USGS) for some large countries, allowing us to further investigate the impact of including IEAS data where available. Thus, we analyzed the global patterns of established alien fish species, with and without IEAS data. By re-analyzing the data used by Dawson et al. (2017) and complementing it with other three

publicly available datasets for three representative countries—China, Japan and South Africa, we demonstrate that the inclusion of IEAS data significantly alters the designated global hotspots of alien fish invasions, which may have significant implications for future invasive species and macroecological research. Finally, we highlight emblematic examples of IEAS, as well as their vectors of introduction and impacts.

Methods and analyses including IEAS in the EAS global hotspots

We used the same data sources and geopolitical units used by Dawson et al. (2017). However, data concerning IEAS, which was left out of their analysis, were also collected for Brazil and the USA. In addition, we also compiled new data for EAS from information publically available for South Africa (Picker and Griffiths 2011), Japan (available in Matsuzaki et al. 2013) and China (available in Kang et al. 2014), all including IEAS. We used these data to propose novel hotspots for EAS using the same approach as that described in Dawson et al. (2017). To quantify the difference between analyses using only EAS and analyses including EAS and IEAS, we calculated a delta value (i.e., $\text{delta} = \text{IEAS richness} - \text{EAS richness}$). Delta was interpreted as the effect of IEAS on the global pattern of EAS for freshwater fish (Table S1, Supplementary material). We then produced a map including IEAS based on the map presented by Dawson et al. (2017), to visualize differences in global hotspots of EAS for freshwater fish (Fig. 1). Finally, we compiled examples of IEAS in published papers, as well as their vectors of introduction and impacts, to demonstrate the range of impacts that might be missed when excluding IEAS data from analysis (Table S2, Supplementary material).

Results including IEAS in the EAS global hotspots

The data clearly show that the global hotspots of EAS for freshwater fish species are different from those proposed by Dawson et al. (2017). Hot and cold spots have changed spatially (States in Brazil, and Provinces in Japan, South Africa and China), especially in the order of magnitude (USA) (Fig. 1 and Table S1 in Supplementary material). In decreasing order, USA, Brazil, Japan, China and South Africa had major changes the numbers of invasive species as indicated by the delta values (Table S1 in Supplementary material). Results of the literature review indicated that the major vectors for the IEAS were sport fishing and fish farming, both causing substantial negative impacts at the community level (Table S2, Supplementary material).

Arguments for including IEAS in the EAS global hotspots

In general, how we define aliens (e.g. including intra-country aliens) influences how we count non-natives and recognize invisibility (Guo and Ricklefs 2010). Consequently, upcoming records and analysis of establishment, invasion patterns and management of non-natives and particularly EAS global hotspots must account for such biases in quantifying and consider the IEAS fraction. Problems associated with IEAS in freshwater ecosystems are more common in large nations, especially considering the negative impacts of massive invasions, such as those experienced in Brazil (Vitule et al. 2012; Frehse et al.

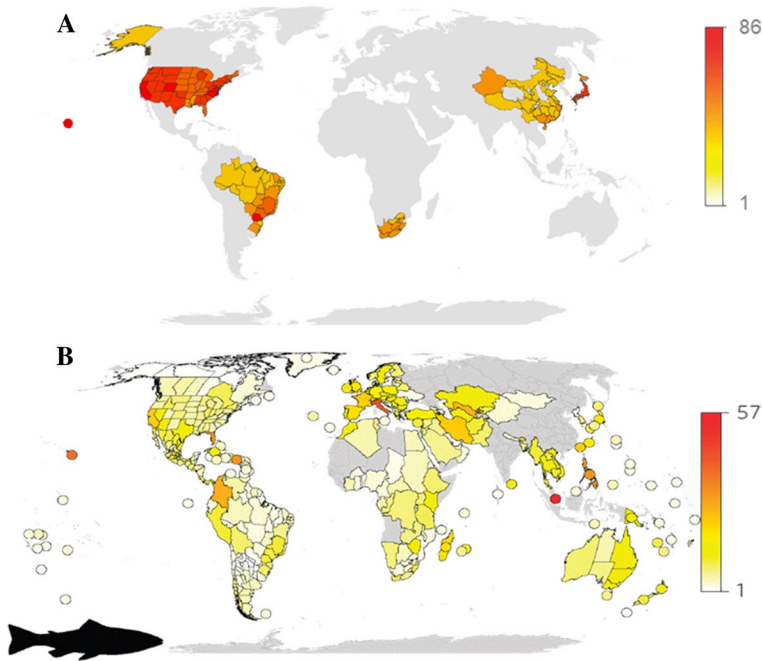


Fig. 1 Established Alien Species (EAS) richness in the TDWG level-4 regions based on data available for freshwater fish. **a** Our analyses using the Dawson et al.'s data source but considering Intra-Country Established Alien Species (IEAS) for Brazil and USA; for South Africa we used Picker and Griffiths (2011), for China we used Kang et al. (2014), and for Japan, Matsuzaki et al. (2013). **b** Dawson et al.'s results for alien fish species (without taking IEAS into consideration)

2016; Pelicice et al. 2017; Bezerra et al. 2019), China (Kang et al. 2017; Liu et al. 2017), Japan (Watanabe 2010; Matsuzaki et al. 2013), South Africa (Weyl et al. 2016), and other countries (Estes et al. 2011) (see Table S2 in Supplementary material for examples). Such impacts include, but are not restricted to, the depletion of native populations (Pelicice and Agostinho 2009), the collapse of subsistence fisheries (Agostinho et al. 2007), genetic introgression (Vitule et al. 2009), cascading effects and landscape-level modification (Estes et al. 2011). IEAS are identified in many regions as the main component of the biotic homogenization process (e.g., in Japan—Watanabe 2010; Brazil—Vitule et al. 2012; China—Liu et al. 2017; and Europe—Sommerwerk et al. 2017). An emblematic example is the construction of the Itaipu Dam, a large dam in the Atlantic Rainforest biome, a global hotspot for conservation (Myers et al. 2000). This large dam caused the drowning of the ‘Sete-Quedas’ Falls, thereby eliminating one of the largest falls in terms of volume of water (Skóra et al. 2015). As a consequence, a major natural biogeographical barrier between the upper and lower Parana River ecoregions was disrupted, allowing the massive introduction of IEAS. At least 50 fish species were introduced from the lower to the upper Parana ecoregion, causing fish faunal homogenization in the region (Vitule et al. 2012).

Frequently, non-native fish species are introduced in developing countries to support aquaculture (FAO 2016; Lima-Junior et al. 2018; Bezerra et al. 2019), which results in large scale introductions of the same species over the entire country. For instance, an exceptional case of IEAS is the invasion of the southeastern Amazon Basin by *Arapaima gigas*

Schinz, 1822 (Arapaimatidae). In the past few years non-native populations of *Arapaima gigas*, commonly known in Brazil as pirarucu, expanded their distribution upstream into the Madeira River rapids, where it is now an emblematic and problematic invasive species (Doria et al. 2019). *Arapaima gigas* was previously introduced into the same macro-basin and biome (i.e., Amazon), but in different and isolated parts of the larger basin (or ecoregion, see Abell et al. 2008). *Arapaima* is a good example of a fish species increasing its invasion range (e.g., Brazil, Peru and Bolivia) and affecting traditional fisheries since populations are declining within its native range in the central Amazon (Miranda-Chumacero et al. 2012). The current invasion is associated with escapes of individuals from Peruvian fish farms upstream in the Madeira River Basin. These powerful rapids had served as a major geographical barrier to the invasion and establishment *A. gigas* until they were eliminated by the construction of the Santo Antônio and Jirau dams in 2011 (Doria et al. 2019). Since the construction of these dams, the fisheries reports for Madeira River have been noteworthy because of the decrease in traditional commercial fish species, a decrease now reinforced by the presence of *A. gigas* and negative impacts associated with it.

Neither of these examples would have been noted in an analysis based strictly on geographical boundaries. Therefore, just by refining the inclusion criteria (i.e., adding IEAS) we can gain some insight into the scope of the problem and the importance of IEAS in the global distribution of established alien freshwater fish species. We suggest that experts in other taxonomic groups analyzed by Dawson et al. (2017) should carefully take into account IEAS in their future research. Of course, to be able to include IEAS data, fine-scale distribution data needs to be available in accessible databases. Examples of such integrated open-access databases for invasive species data include the NGO 'I3N' (<http://i3n.institutohorus.org.br/www/>) and the network 'INVASIVESNET' (<https://www.invasivesnet.org/>). Although there remain some challenges in the representation of certain taxonomic groups and sampling bias, the use of big data is likely to generate conclusions that are more robust. Integrating local invasive species data with data from global-level species distribution databases such as GBIF (<https://www.gbif.org/>) and FishBase (<http://www.fishbase.org/>) has the potential to disentangle the factors involved in invasive species establishment.

We suggest that finer-scale distribution data will enhance our ability to identify global hotspots of EAS, especially with respect to IEAS in the most biodiverse areas of the world. Certainly, in large developing countries such as Brazil and China there are still data gaps regarding invasive species distribution, but such countries are conspicuous donors and global invasion hotspots (Vitule et al. 2009; Watanabe 2010; Liu et al. 2017; Pelicice et al. 2017; Bezerra et al. 2019), and need to consider the substantial impact of intra-country introductions.

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